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REVIEW ARTICLE

Aquaporins: Multifunctional Players in Plant Growth, Development and Stress Responses

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Abstract

Aquaporins are small membrane proteins belonging to the group of Major Intrinsic proteins (MIPs) that facilitate the transport of water and small molecules across biological membranes. They were initially identified as water channels and later it has become clear that they also play important roles in several other physiological processes in plants. Plants have different types of aquaporins in terms of their location, gating properties, and solute specificity and can mainly divide into four major subfamilies. They are tonoplast intrinsic proteins (TIPs), nodulin26-like intrinsic proteins (NIPs), plasma membrane intrinsic proteins (PIPs), and the small basic intrinsic proteins (SIPs). All these aquaporins play a variety of physiological activities at all stages of plant growth and development. Also, they are believed to play a significant part in the plant's defense mechanisms against biotic and abiotic stresses. This review comprehensively addresses the roles of diverse aquaporin homologs in growth and development and their response to different environmental factors.

Keywords
aquaporins, biotic stress, development, growth, water

Introduction

Aquaporins (AQPs) are widely distributed membrane channel proteins that enable the transportation of water and other molecules across the plasma membrane and other cell membranes. The unique structure of aquaporin makes them important in several physiological activities in plants. They are located in the plasma membrane,

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endoplasmic reticulum, vacuoles, and plastids and are classified into different subfamilies including tonoplast intrinsic proteins, the nodulin26-like intrinsic proteins, plasma membrane intrinsic proteins, small basic intrinsic proteins, and uncategorized (X) intrinsic proteins (XIPs) (Anderberg, Kjellbom and Johanson, 2012). Among all PIP consists of larger members and are mainly subdivided into two *PIP1* and *PIP2*. *PIP1* has poor water transportation ability whereas *PIP2* possesses more effective water transport activity. Several studies have revealed that TIPs are responsible for the high rate of water and solute transportation through the tonoplast. As the name implies small intrinsic proteins have the smallest molecules among four subfamilies and their role in plants is not clearly defined yet. NIPs are responsible for the transportation of different molecules including water, glycerol, NH3, and other minor solutes (Maurel *et al.*, 2015).

Many pathogens are likely to infect plants, thus plants evolve defense mechanisms to fend them off. It has become evident that AQPs play a significant role in host-pathogen contact (S Tian *et al.*, 2016). By triggering a systemic acquired resistance (SAR) and immune responses that are activated by pathogen-associated molecular patterns (PAMP) in plants, AQPs can mediate the transport of H2O2 across plasma membranes (PMs) and contribute to the activation of plant defenses. Therefore, it is crucial to address the roles of AQPs in the plant immunity (Dodds and Rathjen, 2010). For more than a decade, plant scientists have been interested in the involvement of AQPs in several physiological processes, particularly those involving abiotic stresses. Aquaporins are responsible for maintaining osmotic pressure, and hydraulic conductivity of plant tissues and are thus, considered as potential regulators of plant-water interactions (Alexandersson et al., 2005). Also, AQPs have been discovered to play roles in growth and development, including seed germination, root growth, leaf expansion, and reproductive organ development (Liu *et al.*, 2007).

Information on the molecular makeup, function, and regulation of plant AQPs have been studied by many scientists. Therefore, the focus of this study is to summarize the different roles of aquaporins in plants.

1. Aquaporins in plants

Aquaporins (AQPs) are membrane channel proteins that can be found in almost all living organisms. It was first discovered by Peter Agre and Preston, who were working on red blood cell membrane proteins in human erythrocytes (Preston and Agre, 1991). They belong to one of the highly conserved membrane protein classes known as Major Intrinsic proteins (MIPs). The arrangement of six transmembrane alpha-helices with N and C termini located at the cytoplasm gives aquaporins a characteristic nature. Those transmembranes are connected by internal and external loops which are hydrophobic. Aquaporin polypeptide chains are composed of amino acid sequences which are arranged symmetrically. This symmetrical nature allows aquaporins to mediate bi-directional water flow. One of the most conserved amino acids, asparagine-proline-alanine (NPA) located at the first intracellular and the third extracellular loop to form a narrow,

water-filled channel (Reizer, Reizer and Saier, 1993). In addition to water, it is known that aquaporins are the most prominent transmembrane transporters of CO2, NH3, glycerol, urea, metalloids, and reactive oxygen species (ROS) (Maurel *et al.*, 2015). Scientists have found that there are fourteen types of aquaporins in mammals. But plants have more diversity in terms of aquaporins variety (King, Kozono and Agre, 2004). A higher degree of cell compartmentation and a greater need for precise water regulation are the causes of plants' increased aquaporin variety, which helps them adapt to shifting environmental conditions. They are in a variety of isoforms that reflect a wide range of transport selectivity, cellular localizations, and regulatory characteristics. For instance, thirty-five sequences which are similar to aquaporin genes were identified in *Arabidopsis thaliana* whereas, thirty-six and thirty-three sequences have been found in maize and rice accordingly (King, Kozono and Agre, 2004). Aquaporins are located mainly in the plasma membrane and in addition to that they can be localized in the endoplasmic reticulum, vacuoles, and plastids.

2. The diversity of aquaporin gene family in plants

The researchers have identified over 30 isoforms of aquaporins in higher plants which can be categorized under four major subfamilies. They are tonoplast intrinsic proteins (TIPs), nodulin26-like intrinsic proteins (NIPs), plasma membrane intrinsic proteins (PIPs), and the small basic intrinsic proteins (SIPs). In addition to that, another subgroup called uncategorized (X) intrinsic proteins (XIPs) was discovered recently (Anderberg, Kjellbom and Johanson, 2012). TIPs, NIPs, and PIPs are conserved in all plants while some subclasses such as XIPs, Hybrid Intrinsic Proteins (HIPs), or Glomerular Intrinsic Proteins (GIPs were lost during the evolution of certain plant species.

2.1. Plasma membrane intrinsic proteins (PIPs)

Among all subfamilies, the PIP group comprises the largest number of members. As the name implies PIPs are found in the plasma membrane. The properties of cellular water uptake, water loss, and hydraulic conductivity are determined by PIPs. This subfamily can be further classified as *PIP1* and *PIP2*. The amino acid residues present in both *PIP1* and *PIP2* are similar. But their cellular activity and permeability appear to be different.

PIP1 aquaporins showed relatively poor water permeability in a variety of functional characterization assays. However, the outcomes of several experiments suggested that they were involved in plant water interactions. For example, *PIP1* antisense Arabidopsis seedlings resulted in poor hydraulic conductivity and lower water permeability of roots compared to controls, indicating their contribution to root water transport (Martre *et al.*, 2002). In addition to that, *PIP1*s should be activated in plants to transport other molecules such as CO2, NH3, and urea. *PIP1* aquaporins can modify their functions according to the requirement of plant tissues. For instance, *PIP1*s may serve as tiny solute or gas transporters in leaf cells while the same molecules may exhibit water channel activity in root plasma membranes through changes or inter-

actions with other aquaporins. Many studies have shown that aquaporins from the *PIP2* subfamily have more effective water transport activity than those from the *PIP1* family, which may be because *PIP2*s have a distinct molecular structure than *PIP1* isoforms. The first eight amino acids have longer carboxyterminal termini, and shorter amino termini. Previous studies indicate that *PIP2* aquaporins have five to twenty-fold higher water permeability in comparison to control values. Members of the *PIP2* subfamily and their involvement in various physiological processes have so far been identified in many species. The proteins may have a role in cellular water transport in roots, leaves, reproductive organs, and seed germination (Martre *et al.*, 2002).

2.2. Tonoplast intrinsic proteins (TIPs)

Tonoplast is a semi-permeable membrane surrounding the vacuoles which involve turgor regulation, cell signaling, and degradation. Aquaporin that was found in the *TP25* protein group in seeds of *P. vulgaris* was the first TIP aquaporin reported in plants (Marzena et al 2020).

TIPs are responsible for the high rate of water and solute transportation through the tonoplast. A study was performed to examine the rates of water transfer in pure tobacco tonoplast vesicles and found that urea or glycerol was more permeable through tonoplast than plasma membrane vesicles (Gerbeau et al., 1999). *NtTIPa* is one of the TIP homologs that was identified in *Xenopus* oocytes which have high permeability to water, urea, and glycerol. Furthermore, different TIP isoforms that were isolated from *Arabidopsis thaliana* were given similar results(Liu and Liu, 2003). Therefore, the studies have proven that TIPs play a significant role in equilibrating urea concentrations between different cellular compartments in addition to water regulation.

2.3. Small intrinsic proteins (SIPs)

The small intrinsic proteins are composed of the smallest molecules among four subfamilies. Not only that, the number of groups present in SIPs is also the lowest. It has only three members in *Arabidopsis* (*AtSIP1;1, 1;2*, and *2;1*) and two members in *Oryza sativa* (*OsSIP1;1* and *2;1*). The structural differences in SIP include, 1) variation in initial NPA motifs of different SIPs 2) shorter N-terminal tails with similar C-terminal tails as those in PIPs and TIPs 3) a large number of basic molecules such as Lysine, and 4) higher isoelectric points compare to other subfamilies which make them unique to the other subfamilies (Venkatesh, Yu and Park, 2013).

2.4. Nodulin 26-like intrinsic proteins (NIPs)

The first member of the NIP family was discovered from the soybean nodulin 26 during the formation of symbiotic nitrogen-fixing root nodules (Fortin, Morrison and Verma, 1987). Experiments have shown that this group is responsible for the transportation of different molecules, and mediates the bidirectional transit of water, glycerol, NH3, and other minor solutes between the cytoplasm of plants and sym-

biotic bacteroid. NIP genes that were isolated from *A. thaliana* are categorized into two subgroups as NIP group I and NIP group II. The main two structural differences between the two groups are the aromatic Arginine selectivity filter close to the NPA pore region in *NIP II* and the conserved CDPK phosphorylation site in *NIP I* which cannot be found in other groups (Fortin, Morrison and Verma, 1987). Since NIP was discovered to be crucial for boron transport in *Arabidopsis* plants, it has recently received attention (Takano *et al.*, 2006).

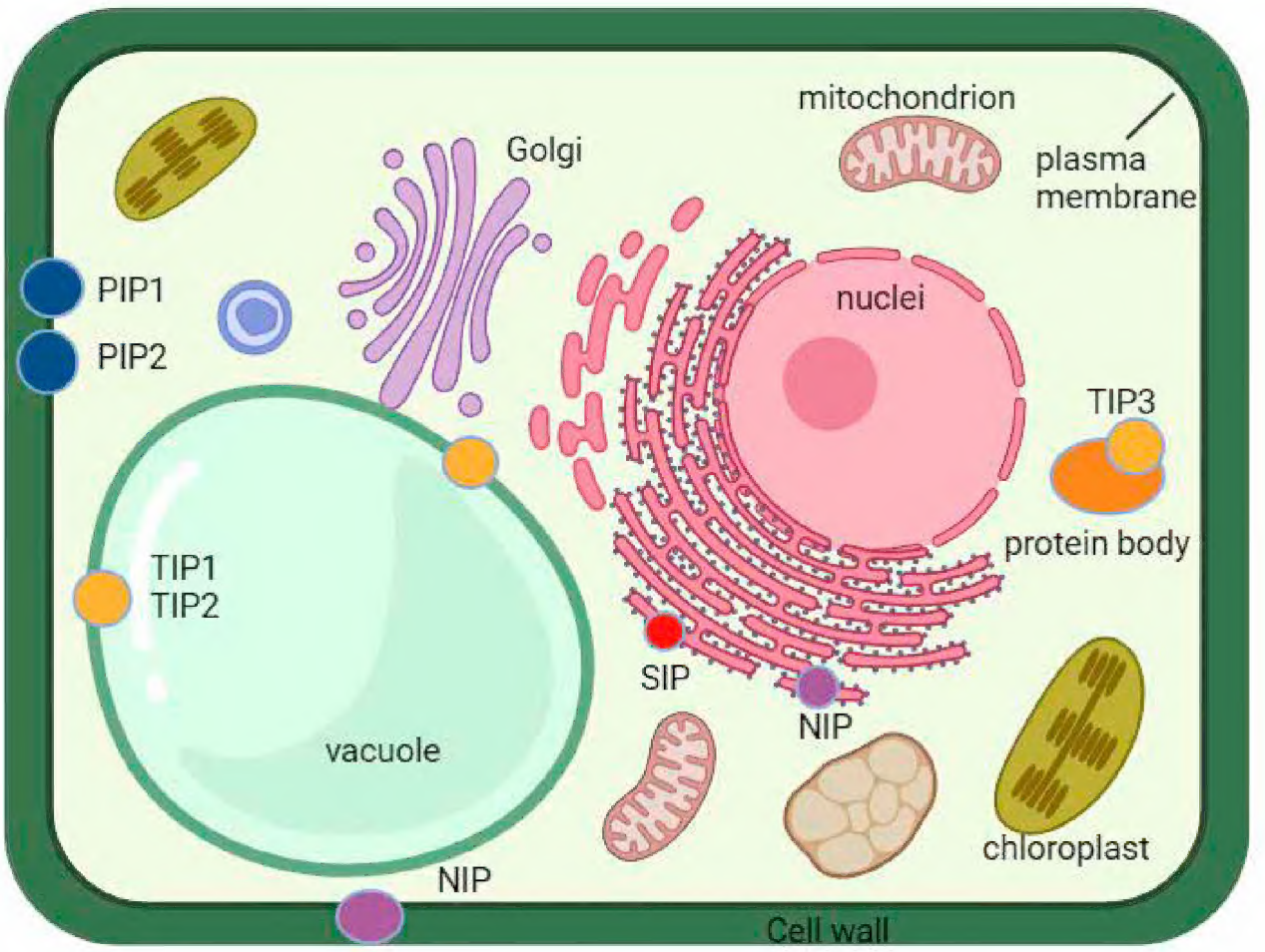

Fig. 1. A diagram of Aquaporins found in different organelle membranes

Small basic intrinsic proteins (SIPs), tonoplast intrinsic proteins (TIPs), nodulin 26-like intrinsic proteins (NIPs) ,and plasma-membrane intrinsic proteins (PIPs) are all found on the ER membrane, tonoplast, and plasma membranes respectively (Rodrigues *et al.*, 2017).

3. Roles of Aquaporins in Plant-Pathogen Interaction

Plant pathogens such as viruses, bacteria, and fungus have evolved various strategies to attack plants causing a variety of diseases that can lead to significant economic losses (Savary *et al.*, 2019). Plants have developed functional innate immune systems against pathogens. The very first compartment where plant-pathogen interaction takes place is in the plasma membrane. Their activity mostly depends on the activities

Table 1. Characteristics of major aquaporin subfamilies in plants

Subfamily	Cellular locations	Physiological functions
PIP	Plasma membrane roots, shoots and leaf tissues	transport of water and other small neutral molecules such as glycerol, H2O2, and carbon dioxide across cellular biological membranes
TIP	Vacuolar membranes in roots, seeds, and leaves	precisely regulating the movement of water, glycerol, urea, ammonia, hydrogen peroxide, and formamide
SIP	Endoplasmic Reticulum (ER) membrane	Involved in water activities in plants through the water channels in ER The membrane remains to be examined
NIP	Membranes in root nodules	transportation of different molecules, mediate the bidirectional transit of water, glycerol, NH3, and other minor solutes

of membrane proteins and other biomacromolecules. Previous studies have revealed that aquaporins play a significant role in plant defense mechanisms against pathogens (Shan Tian *et al.*, 2016).

3.1. Functions of aquaporins in the plant immunity

Plants have developed mechanisms against pathogens called pathogen-associated molecular patterns (PAMPs) using different components of various organisms such as chitin from fungus, bacterial flagellin, and harpin proteins. The molecular mechanisms are further triggered by PAMP-triggered immunity (PTI) which leads to activate various defense reactions. Those reactions include the production of reactive oxygen species, the secretion of antimicrobial secondary metabolites the activation of ion fluxes and conserved mitogen-activated protein kinase (MAPK) signaling cascades, stomatal closure, and cell wall strengthening. Although plants have developed many mechanisms, pathogens can still attack plants by suppressing PTI by delivering effectors proteins to plants. To counter this, plants have evolved a new, more potent immune response known as effector-triggered immunity (ETI), which involves localized cell death. This is also known as the hypersensitive response (HR), and systemic acquired resistance (SAR) (Dodds and Rathjen, 2010).

Reactive oxygen species are formed at the infection site as a defense mechanism after the pathogens have been attacked (Wang *et al.*, 2019).The successful detection of pathogen invasion is reflected by the sudden generation of ROS such as H2O2. In turn, it triggers several immunological reactions, including PTI and SAR, to control plant disease resistance (Torres, 2010). NADPH oxidase which is present in the plasma membrane (PM) induces ROS burst in plants by transferring electrons to apoplastic oxygen. Then superoxide dismutase catalyzes the production of H2O2. The resulting H2O2 is then immediately translocated to the cytoplasm via a plasma membrane. At-PIP1;4, a member of the PIP family in *Arabidopsis*, has recently been shown to be essential for the movement of H2O2 across the PM (Shan Tian *et al.*, 2016). Following this procedure, various downstream defense responses happened, such as the production of callose by inducing the expression of glucan synthase-like 5 *GSL5*, the activa-

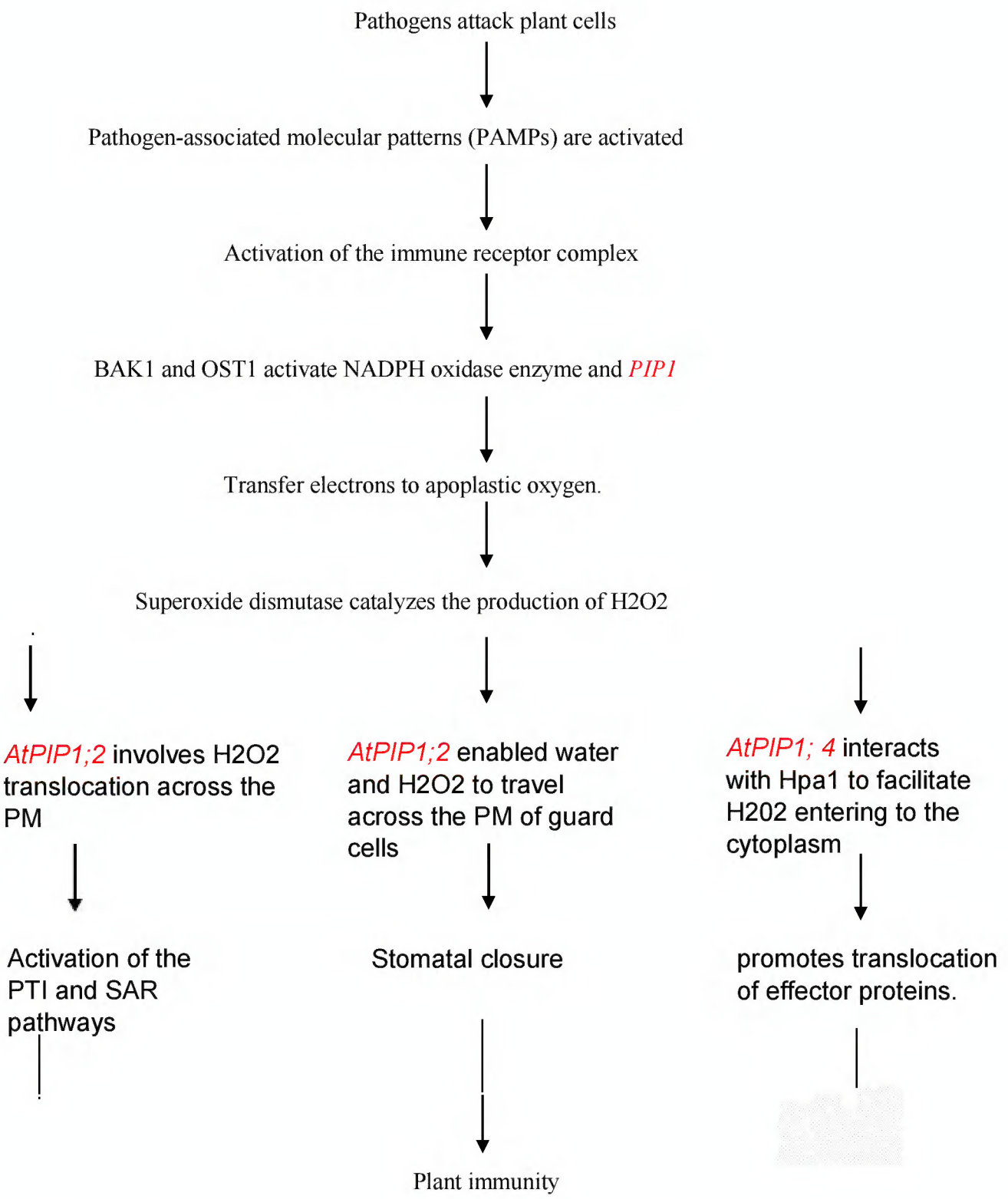
Pathogens attack plant cells
Pathogen-associated molecular patterns (PAMPs) are activated
Activation of the immune receptor complex
BAK1 and OST1 activate NADPH oxidase enzyme and PIP1
Transfer electrons to apoplastic oxygen.
Superoxide dismutase catalyzes the production of H2O2
AtPIP1;2 involves H2O2 translocation across the PM
AtPIP1;2 enabled water and H2O2 to travel across the PM of guard cells
AtPIP1; 4 interacts with Hpa1 to facilitate H202 entering to the cytoplasm
Activation of the PTI and SAR pathways
Stomatal closure
promotes translocation of effector proteins.
Plant immunity

Fig. 2. The flow of the involvement of aquaporins in mediating plant immunity

tion of the nonexpresser of pathogenesis-related genes 1 *NPR1* and *PR* genes, and the activation of conserved MAPK signaling cascades. H2O2 is unable to enter the cells due to the presence of 4 knockout mutants in AtPIP1, leading to high amounts of H2O2 accumulated within apoplastic areas. It creates an unfavorable environment for pathogens. Therefore, these studies have proven that the *AtPIP1;2* aquaporin group is responsible for the translocation of apoplastic H2O2 to the activation of the PTI and SAR pathways in response to PAMPs. Moreover, it has been shown that many other Aquaporins in plants, such as PIPs and TIPs, mediate the transport of H2O2 across cell membranes (Dynowski *et al.*, 2008). Importantly, the structural arrangement might make it much easier to understand how AQPs work. The recent studies on structural

characteristics of AQPs for controlling H2O2 transport may help to understand the complex mechanisms involving AQPs in host-pathogen interaction. In turn, H2O2 also controls the expression, activity, and localization of particular AQPs and modifies their ability to transport H2O2, which helps to explain the immunological responses that H2O2-induced stress in plants causes (Kapilan, R., Vaziri, M. & Zwiazek, J.J 2018).

In addition, those plants have an ability to close their stomata in response to pathogen invasion as a part of their natural immunity. According to the literature the stress hormone 'Abscisic Acid' (ABA) is known to play a key role in controlling stomatal closure (Rodrigues *et al.*, 2017). An experiment on stomatal closure in *Arabidopsis* revealed that *AtPIP1;2* enabled water and H2O2 to travel across the PM of guard cells to facilitate pathogen-induced stomatal closure (Rodrigues *et al.*, 2017). The activation of AtPIP1;2 to transport H2O2 in response to ABA signaling and PAMP identification may be caused by the phosphorylation of *AtPIP1;2* at Ser121 by Brassinosteroid Insensitive 1-associated Receptor Kinase 1 (BAK1) and/or Open Stomata 1 (OST1). These results proved that the PIP1 group is involved in the regulation of stomatal activity in response to pathogen attacks which ultimately leads to PAMP- triggered immunity. Furthermore, pathogenic bacteria can secrete a protein called harpin (Hpa1) which has an ability to create pores through cell membranes and thus promotes translocation of effector proteins. Studies have shown that AtPIP1; 4 interacts with Hpa1 to facilitate H202 entering the cytoplasm which leads to the initiation of immune response (Li *et al.*, 2019).

4. Roles of Aquaporins in Plant–Water Relations

Plants absorb water through the soil in order to carry out all physiological functions including, photosynthesis, transportation of minerals and nutrients, and growth. Plants absorb water using three major pathways: the apoplastic pathway, the symplastic pathway, and the transcellular pathway (Steudle and Peterson, 1998). Transportation of water for long distances occurs through the apoplastic route whereas the transportation of water for shorter distances occurs through the symplastic, and the transcellular pathway (Kaldenhoff *et al.*, 2008). Since aquaporins involve in maintaining osmotic pressure, hydraulic conductivity of plant tissues, and elongation of cells, they can be considered as potential regulators of plant-water interactions.

4.1. Roles of aquaporins under drought stress conditions

Several studies have proven that AQPs are responsible for water deficit and play a crucial role in drought stress tolerance. Moreover, PIPs and TIPs play a significant role in mediating water intake and transcellular water flow in the roots of the majority of plant species as they are the most abundant aquaporin groups in PM and tonoplast. They are regulated at both transcriptional and post-translational levels. Many studies proved that aquaporins in different subfamilies exhibited different expressions in response to drought stress, indicating that they play distinct roles in stress responses.

Previous studies discovered that the majority of PIP and some TIP genes have high levels of expression, while NIP genes have extremely low expression against drought stress (Alexandersson *et al.*, 2005). Also, the study revealed that all PIP genes except *AtPIP1; 4* and *AtPIP2; 5* are down-regulated in drought stress response in leaves while others are up-regulated. This is because some plants downregulate some AQPs to reduce their membrane water permeability in order to prevent excessive water loss, while others contend that plants enhance membrane water permeability by up regulating AQPs during conditions of water shortage. Additionally, *AtPIP2; 6* and *AtSIP1; 1* are expressed constantly, indicating they are not affected by the drought stress. According to several studies on *Arabidopsis,* PIPs are the most susceptible aquaporin subfamily to drought stress which undergo transcriptional down-regulation (Jang *et al.*, 2004). Although the expression of different genes between *Arabidopsis* accessions is similar, other plant species show differential responses by the same aquaporin homolog among the same plant species (Vandeleur *et al.*, 2009).

Several investigations have been conducted to find out the cellular and molecular mechanisms of AQPs under stressful circumstances. A study on spinach showed that *SoPIP2;1* aquaporin underwent a conformational change to prevent water flow through the membrane (Jang *et al.*, 2014). This mechanism is called 'gating' which happens by dephosphorylation of certain serine residues. In addition to that, the regulation of different PIPs is significantly influenced by ABA, a key participant in drought stress signaling. The responsiveness of PIP genes to water stress and ABA is different as it involves both ABA dependent and ABA-independent signaling mechanisms. ABA aids in modulating the expression of numerous PIPs in response to drought. ABA synthesizes in plant tissues when there is a water deficit which may lead to down-regulation of PIPs. It decreases the osmotic water permeability (Pf) of those cells and thus, reduces the flow of water into the leaf (Meinzer, 2002). In contrast, aquaporin response against drought stress is highly variable as it depends on several factors such as type of tissue, species, stress levels, and other environmental factors.

4.2. Roles of aquaporins in salt stress

Salt stress is the stress that causes a disruption of the osmotic balance of cells due to the mix of water and ions. Most of the salt stress responses in plants are associated with drought stress mechanisms. PIPs and TIPs are mainly involved in regulating the salt stress of plants. According to the previous studies, aquaporins appear to be relocalized or redistributed in response to high salt concentrations. For example, *Arabidopsis* has also demonstrated that salt stress-induced re-localization of *AtTIP1;1* into intravacuolar invaginations. In addition to redistribution, endocytosis of PIPs via a clathrin-dependent pathway or a salt-stimulated membrane raft-associated pathway is another mechanism that controls PIP abundance in the plasma membrane(Gao *et al.*, 2010). For instance, *Arabidopsis* also internalized *PIP2;1-GFP* and relocalized a *TIP1;1-GFP* into intracellular spherical formations in response to stress (Boursiac *et al.*, 2005).

4.2. Roles of aquaporins in cold stress

Cold stress is a significant factor that determines the growth and development of plants. Similar to other stresses PIPs and TIPs are the major groups that mediate cold stress. When exposed to low temperatures, plant roots express more aquaporins, which may control the response of aquaporins to cold stress by increasing root hydraulic conductivity. Different reactions have been seen when exposed to cold stress for short and long periods. Aquaporin expression has also been connected to the recovery from cold stress, particularly in PIPs. For example, *MusaPIP1;2* and *MusaPIP1;2* of transgenic banana plants were upregulated while *OsTIP1;1* and *OsTIP2;2* of rice were significantly downregulated against cold stress(Sakurai *et al.*, 2005).

5. Roles of aquaporins in vegetative growth

5.1. Seed germination

The process of seed germination includes imbibition which results in rehydration and expansion of the cells, followed by vacuole biosynthesis, mobilization of reserves during seed germination, and development of the embryo axis into a seedling. AQPs are facilitated most of these steps by up-taking water (Hoai *et al.*, 2020). Previous research has found that several *TIP1, TIP2*, and PIP genes are up-regulated during seed germination in many plants, while TIP3s are down-regulated, emphasizing their potential roles in germination. In addition to that genetic evidence supports the idea that AQPs are necessary for seed germination. For instance, in rice, the rate of seed germination was reduced due to the knockdown of *OsPIP1;3. OsPIP1* overexpression at a moderate or low level also dramatically increases amylase activity and seed germination rates (Liu *et al.*, 2007). There are two types of seeds as orthodox and recalcitrant in terms of their survival during drying and freezing. AQPs may serve roles in the germination of both types. For example TIPs (*HvTIP3;1*), are involved in vacuolation and alpha-amylase activity of orthodox seeds (Lee *et al.*, 2015). In recalcitrant seed germination, vacuole enlargement is facilitated by AQPs through the increase in water inflow. For example, *AhTIP2, AhTIP3;1, AhPIP1, and AhPIP2* are up- regulated during seed germination (Obroucheva *et al.*, 2012).

5.2. Root growth

After seed germination, the growth of radicals in orthodox seed plants happens through the fusion of provacuoles to generate large vacuoles while the growth of recalcitrant seed plants happens through the enlargement of existing vacuoles. Large vacuoles are necessary for cell elongation and several experiments prove that TIPs and PIPs are crucial for the synthesis of provacuoles and LVs by transporting water into vacuoles and cytoplasm in order to facilitate root growth (Penfield, 2017). Furthermore, PIPs and TIPs are abundant and enriched in growing root tips, indicating their

significance in root growth. For example, *ZmPIP1; 2, ZmPIP2; 4, and ZmTIP1; 1* are highly expressed in the root growing zone in maize (Hukin *et al.*, 2002). Additionally, AQPs help in root growth by absorbing water and nutrients through root tips.

5.3. Shoot growth

Leaves are important in several physiological processes in plants including photosynthesis, transpiration and respiration. The activity of AQPs is vital for the growth and development of leaves as it facilitates the movement of CO2 and water in leaf cells. Many transcription studies indicate that expression patterns of TIP and PIP genes are correlated with cell water permeability. For instance, In the elongation zones of leaves in maize, *ZmPIP1;1, ZmPIP1;2, ZmPIP1;3, ZmPIP2;1, and ZmPIP2;2* are actively expressed (Besse *et al.*, 2011). APQs also play a role in leaf growth by enlarging the hydraulic conductivity of leaves in growing tissues. An experiment on Sunflower revealed that 25%-50% of leaf hydraulic conductivity depends on APQs activity (Pou *et al.*, 2013).

6. Role of aquaporins in gas permeability of plants

Although the gases like NH3 or CO2 simply diffuse through the lipids of membranes in plants, It was proposed that an increased gas transport rate was controlled by aquaporins (Terashima and Ono, 2002). AQPs form tetramers to facilitate protein activity and stabilization. They serve as a water channel and also help to transfer other volatile materials such as CO2 or NH3. An experiment revealed that the PIP2 subfamily contributes to facilitated CO2 transport in rice). There is evidence that TIPs have the ability to regulate NH3 uptake by changing the membrane permeability (Kapilan, R., Vaziri, M. & Zwiazek, J.J 2008)

Conclusion

AQPs play a significant role in plant growth and development by involving the regulation of several activities. SIPs, TIPs, PIPs, and NIPs are the four main subfamilies of aquaporins which are located in ER membrane, tonoplast and plasma membranes respectively. In contrast, PIP and TIPs are mainly responsible for the transport of water and other small neutral molecules such as glycerol, H2O2, and carbon dioxide across cellular biological membranes and thus, involved in growth and development, plant water interactions, biotic and abiotic stress responses. NIP's role in bidirectional transit of water, glycerol, NH3, and specifically boron between the cytoplasm of plants and symbiotic bacteroides received attention recently. SIP also has an impact on water transportation but its mechanism remains to be examined. Each of these groups plays a significant role in plants and transcriptional studies in different cell types indicate their roles in different processes. Transcriptional studies revealed that some genes are

up-regulated during certain physiological activities while others are down-regulated. Gene expression depends on several factors including, the type of aquaporin involved, type of tissue, and the species.

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References

Alexandersson E., Fraysse L., Sjövall-Larsen S., Gustavsson S., Fellert M., Karlsson M., ... & Kjellbom P. 2005. Whole gene family expression and drought stress regulation of aquaporins. Plant molecular biology 59(3), 469-484.

Anderberg H. I., Kjellbom P., & Johanson U. 2012. Annotation of Selaginella moellendorffii major intrinsic proteins and the evolution of the protein family in terrestrial plants. Frontiers in plant science 3, 33.

Besse M., Knipfer T., Miller A. J., Verdeil J. L., Jahn T. P., & Fricke W. 2011. Developmental pattern of aquaporin expression in barley (*Hordeum vulgare* L.) leaves. Journal of Experimental Botany 62(12), 4127-4142.

Boursiac Y., Chen S., Luu D. T., Sorieul M., van den Dries N., & Maurel C. 2005. Early effects of salinity on water transport in Arabidopsis roots. Molecular and cellular features of aquaporin expression. Plant physiology 139(2), 790-805.

Dodds P. N., & Rathjen J. P. 2010. Plant immunity: towards an integrated view of plant–pathogen interactions. Nature Reviews Genetics 11(8), 539-548.

Dynowski M., Schaaf G., Loque D., Moran O., & Ludewig U. 2008. Plant plasma membrane water channels conduct the signalling molecule H2O2. Biochemical Journal 414(1), 53-61.

Fortin M. G., Morrison N. A., & Verma D. P. S. 1987. Nodulin-26, a peribacteroid membrane nodulin is expressed independently of the development of the peribacteroid compartment. Nucleic acids research 15(2), 813-824.

Gao Z., He X., Zhao B., Zhou C., Liang Y., Ge R., ... & Huang Z. 2010. Overexpressing a putative aquaporin gene from wheat, TaNIP, enhances salt tolerance in transgenic Arabidopsis. Plant and Cell Physiology 51(5), 767-775.

Hoai P. T., Tyerman S. D., Schnell N., Tucker M., McGaughey S. A., Qiu J., ... & Byrt C. S. 2020. Deciphering aquaporin regulation and roles in seed biology. Journal of Experimental Botany 71(6), 1763-1773.

Hukin D., Doering-Saad C., Thomas C., & Pritchard J. 2002. Sensitivity of cell hydraulic conductivity to mercury is coincident with symplasmic isolation and expression of plasmalemma aquaporin genes in growing maize roots. Planta 215(6), 1047-1056.

Jang H. Y., Rhee J., Carlson J. E., & Ahn S. J. 2014. The Camelina aquaporin CsPIP2; 1 is regulated by phosphorylation at Ser273, but not at Ser277, of the C-terminus and is involved in salt- and drought-stress responses. Journal of plant physiology 171(15), 1401-1412.

Jang J. Y., Kim D. G., Kim Y. O., Kim J. S., & Kang H. 2004. An expression analysis of a gene family encoding plasma membrane aquaporins in response to abiotic stresses in Arabidopsis thaliana. Plant molecular biology 54(5), 713-725.

Kaldenhoff R., RIBAS-CARBO M. I. Q. U. E. L., Sans J. F., Lovisolo C., Heckwolf M., & Uehlein N. 2008. Aquaporins and plant water balance. Plant, Cell & Environment 31(5), 658-666.

Kapilan R., Vaziri M. & Zwiazek J.J. Regulation of aquaporins in plants under stress. Biol Res 51, 4 (2018). https://doi.org/10.1186/s40659-018-0152-0

King L. S., Kozono D., & Agre P. 2004. From structure to disease: the evolving tale of aquaporin biology. Nature reviews Molecular cell biology 5(9), 687-698.

Lee S. E., Yim H. K., Lim M. N., Yoon I. S., Kim J. H., & Hwang Y. S. 2015. Abscisic acid prevents the coalescence of protein storage vacuoles by upregulating expression of a tonoplast intrinsic protein gene in barley aleurone. Journal of Experimental botany 66(5), 1191-1203.

Li P., Zhang L., Mo X., Ji H., Bian H., Hu Y., ... & Dong H. 2019. Rice aquaporin PIP1; 3 and harpin Hpa1 of bacterial blight pathogen cooperate in a type III effector translocation. Journal of experimental botany 70(12), 3057-3073.

Liu G. R., & Liu M. B. 2003. Smoothed particle hydrodynamics: a meshfree particle method. World scientific.

Liu H. Y., Yu X., Cui D. Y., Sun M. H., Sun W. N., Tang Z. C., ... & Su W. A. 2007. The role of water channel proteins and nitric oxide signaling in rice seed germination. Cell research 17(7), 638-649.

Martre P., Morillon R., Barrieu F., North G. B., Nobel P. S., & Chrispeels M. J. 2002. Plasma membrane aquaporins play a significant role during recovery from water deficit. Plant physiology 130(4), 2101-2110.

Marzena, Małgorzata, Kurowska. 2020. TIP Aquaporins in Plants: Role in Abiotic Stress Tolerance. doi: 10.5772/INTECHOPEN.94165

Maurel C., Boursiac Y., Luu D. T., Santoni V., Shahzad Z., & Verdoucq L. 2015. Aquaporins in plants. Physiological reviews 95(4), 1321-1358.

Meinzer F. C. 2002. Co-ordination of vapour and liquid phase water transport properties in plants. Plant, Cell & Environment 25(2), 265-274.

Obroucheva N. V., Lityagina S. V., Novikova G. V., & Sin'kevich I. A. 2012. Vacuolar status and water relations in embryonic axes of recalcitrant Aesculus hippocastanum seeds during stratification and early germination. AoB Plants, 2012.

Patricia Gerbeau., Josette Güçlü., Pierre Ripoche., Christophe Maurel. 1999. Aquaporin Nt-TIPa can account for the high permeability of tobacco cell vacuolar membrane to small neutral solutes. Plant Journal doi: 10.1046/J.1365-313X.1999.00481.X

Penfield S. 2017. Seed dormancy and germination. Current Biology 27(17), R874-R878.

Pou A., Medrano H., Flexas J., & Tyerman S. D. 2013. A putative role for TIP and PIP aquaporins in dynamics of leaf hydraulic and stomatal conductances in grapevine under water stress and re-watering. Plant, cell & environment 36(4), 828-843.

Preston G. M., & Agre P. 1991. Isolation of the cDNA for erythrocyte integral membrane protein of 28 kilodaltons: member of an ancient channel family. Proceedings of the National Academy of Sciences 88(24), 11110-11114.

Reizer J., Reizer A., & Saier M. H. 1993. The MIP family of integral membrane channel proteins: sequence comparisons, evolutionary relationships, reconstructed pathway of evolution, and proposed functional differentiation of the two repeated halves of the proteins. Critical reviews in biochemistry and molecular biology 28(3), 235-257.

Rodrigues O., Reshetnyak G., Grondin A., Saijo Y., Leonhardt N., Maurel C., & Verdoucq L. 2017. Aquaporins facilitate hydrogen peroxide entry into guard cells to mediate ABA-and pathogen-triggered stomatal closure. Proceedings of the National Academy of Sciences 114(34), 9200-9205.

Sakurai J., Ishikawa F., Yamaguchi T., Uemura M., & Maeshima M. 2005. Identification of 33 rice aquaporin genes and analysis of their expression and function. Plant and Cell Physiology 46(9), 1568-1577.

Savary S., Willocquet L., Pethybridge S. J., Esker P., McRoberts N., & Nelson A. 2019. The global burden of pathogens and pests on major food crops. Nature ecology & evolution 3(3), 430-439.

Steudle E., & Peterson C. A. 1998. How does water get through roots?. Journal of experimental Botany 49(322), 775-788.

Takano J., Wada M., Ludewig U., Schaaf G., Von Wirén N., & Fujiwara T. 2006. The Arabidopsis major intrinsic protein NIP5; 1 is essential for efficient boron uptake and plant development under boron limitation. The Plant Cell 18(6), 1498-1509.

Terashima I., & Ono K. 2002. Effects of HgCl2 on CO2 dependence of leaf photosynthesis: evidence indicating involvement of aquaporins in CO2 diffusion across the plasma membrane. Plant and Cell Physiology 43(1), 70-78.

Tian S., Torres R., Ballester A. R., Li B., Vilanova L., & González-Candelas L. 2016. Molecular aspects in pathogen-fruit interactions: Virulence and resistance. Postharvest Biology and Technology 122, 11-21.

Tian S., Wang X., Li P., Wang H., Ji H., Xie J., ... & Dong H. 2016. Plant aquaporin AtPIP1; 4 links apoplastic H2O2 induction to disease immunity pathways. Plant physiology 171(3), 1635-1650.

Torres M. A. 2010. ROS in biotic interactions. Physiologia plantarum 138(4), 414-429.

Vandeleur R. K., Mayo G., Shelden M. C., Gilliham M., Kaiser B. N., & Tyerman S. D. 2009. The role of plasma membrane intrinsic protein aquaporins in water transport through roots: diurnal and drought stress responses reveal different strategies between isohydric and anisohydric cultivars of grapevine. Plant physiology 149(1), 445-460.

Venkatesh J., Yu J. W., & Park S. W. 2013. Genome-wide analysis and expression profiling of the Solanum tuberosum aquaporins. Plant Physiology and Biochemistry 73, 392-404.

Wang Y., Ji D., Chen T., Li B., Zhang Z., Qin G., & Tian S. 2019. Production, signaling, and scavenging mechanisms of reactive oxygen species in fruit–pathogen interactions. International journal of molecular sciences 20(12), 2994.